

No longer single! Description of female *Calumma vatosoa* (Squamata, Chamaeleonidae) including a review of the species and its systematic position

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Abstract

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Calumma vatosoa is a Malagasy chameleon species that has until now been known only from the male holotype and a photograph of an additional male specimen. In this paper we describe females of the chameleon *Calumma vatosoa* for the first time, as well as the skull osteology of this species. The analysed females were collected many years before the description of *C. vatosoa*, and were originally described as female *C. linotum*. According to external morphology, osteology, and distribution these specimens are assigned to *C. vatosoa*. Furthermore we discuss the species group assignment of *C. vatosoa* and transfer it from the *C. furcifer* group to the *C. nasutum* group. A comparison of the external morphology of species of both groups revealed that *C. vatosoa* has a relatively shorter distance from the anterior margin of the orbit to the snout tip, more heterogeneous scalation at the lower arm, a significantly lower number of supralabial and infralabial scales, and a relatively longer tail than the members of the *C. furcifer* group. These characters are, however, in line with the species of the *C. nasutum* group. In addition the systematic position of *C. peyrierasi* also discussed, based on its morphology.

Introduction

Madagascar is a hotspot of chameleon diversity and endemism (Tolley et al. 2013). Of the currently described 202 chameleon species, 86 species belong to the four Malagasy genera *Brookesia* Gray, 1865, *Calumma* Gray, 1865, *Furcifer* Fitzinger, 1843, and *Palleon* Glaw, Hawlitschek & Ruthensteiner, 2013, and all but two Comorian species of *Furcifer* are endemic to Madagascar (Glaw 2015). Although the Seychelles chameleon, *Archaius tigris* (Kuhl, 1820), was included in the genus *Calumma* until recently, Townsend et al. (2011) demonstrated that it represents a different African lineage and that *Calumma* is endemic to Madagascar. The Malagasy chameleons were relatively intensively studied in the past (Brygoo 1971, 1978), but still many new species are regularly dis-

covered and described (e. g. Raxworthy and Nussbaum 2006, Gehring et al. 2010, Gehring et al. 2011, Glaw et al. 2012), and several species are only known by a single or a few specimens. Within the genus *Calumma*, currently comprising 33 species (Glaw 2015), *C. hafahafa* Raxworthy & Nussbaum, 2006, *C. linotum* (Müller, 1924), *C. peyrierasi* (Brygoo, Blanc & Domergue, 1974), and *C. vatosoa* Andreone, Mattioli, Jesu & Randrianirina, 2001 are such poorly known species. *Calumma linotum* for example was described on the basis of a single male without locality (Müller 1924) and it took more than 90 years to clarify its identity (Prötzel et al. 2015). In the same way, *C. vatosoa* was known only from the male holotype until Lutzmann et al. (2010) made a further record of *C. vatosoa* and presented a photograph of a male individual from near Ampokafo, approximately 50 km southeast of

the type locality (Forêt de Tsararano). So far, no female individual of this species has been recorded. *Calumma vatosoa* is a medium-sized chameleon species and was tentatively assigned to the *C. furcifer* group (sensu Glaw and Vences 1994) due to the absence of occipital lobes, gular and ventral crests and its markedly acute rostral profile, and greenish colouration (Andreone et al. 2001). These authors did not assign it to the *C. nasutum* group (sensu Glaw and Vences 1994), because of the absence of a rostral appendage, absence of a dorsal crest, and presence of axillary pockets. The *C. nasutum* group was recently found to be non-monophyletic (Tolley et al. 2013) and to include *C. peyrierasi*, a species formerly assigned to the *C. furcifer* group. The hemipenis ornamentation of *C. vatosoa* differs from that of all other species of the genus *Calumma* by the coexistence of three pairs of rotulae (Andreone et al. 2001).

In 1931, Bluntschli collected four female chameleons at Col Pierre Radama that were assigned to *Calumma linotum* by Mertens (1933), despite the absence of a rostral appendage and occipital lobes. Mertens (1933) justified this classification due to the absence of a dorsal crest, larger scales at the extremities, the regular gular folds, and the absence of the rostral appendage in the females. As the proper identification of *C. linotum* was recently clarified (Prötzel et al. 2015), we were able to reassign these female specimens to *C. vatosoa*. In this paper we describe for the first time females of *Calumma vatosoa* including the osteology of the species and review its assignment to the *C. furcifer* group. By identifying and reclassifying these individuals, we correct their taxonomic identity and enhance the knowledge about morphology and distribution of this poorly known species.

Material and methods

We studied the male holotype of *Calumma vatosoa* and three females from the Senckenberg Museum at Frankfurt/Main which were labeled as *C. linotum*. Of the four females originally collected (Mertens 1933) only three are still present in the museum collection. In addition, we investigated the external morphology of one adult male and (if available) one female of the species *C. andringitraense* (Brygoo, Blanc & Domergue, 1974), *C. furcifer* (Vaillant & Grandidier, 1880), *C. gastrotaenia* (Boulenger, 1888), *C. glawi* Böhme, 1997, *C. guillaumeti* (Brygoo, Blanc & Domergue, 1974), *C. cf. marojezense*, *C. tarzan* Gehring, Pabijan, Ratsoavina, Köhler, Vences & Glaw, 2010, and *C. vencesi* Andreone, Mattioli, Jesu & Randrianirina, 2001 of the *C. furcifer* group, and *C. boettgeri* (Boulenger, 1888), *C. fallax* (Mocquard, 1900), *C. gallus* (Günther, 1877), *C. guibei* (Hillenius, 1959), *C. linotum*, *C. nasutum* (Duméril & Bibron, 1836), and *C. vohibola* Gehring, Ratsoavina, Vences & Glaw, 2011 of the *C. nasutum* group. *Calumma cucullatum* (Gray, 1831) is not considered a part of the *C. furcifer* group in the strict sense (see phylogeny in Tolley et al. 2013). In addition *C.*

peyrierasi was investigated according to its phylogenetic position in the *C. nasutum* group – but it is clearly separated from the other species of the *C. nasutum* group (Tolley et al. 2013). The same specimen, which was analysed genetically in Tolley et al. (2013), was used for morphological measurements together with three more specimens of the same series. The other comparative specimens were chosen randomly, if several specimens were available, as typical representatives of their species. The studied specimens originated from the collections of the Museo Regionale di Scienze Naturali, Torino, Italy (MRSN), Senckenberg Museum, Frankfurt am Main, Germany (SMF), and from the Zoologische Staatssammlung München (ZSM), Germany (see Table 1 for details).

The following characters (Fig. 1) were measured with a digital calliper to the nearest of 0.1 mm or counted using a binocular dissecting microscope: snout-vent length (SVL) from the snout tip (not including the rostral appendage) to the cloaca; tail length (TaL) from the cloaca to the tail tip; total length (TL) as a sum of SVL + TaL; ratio of TaL to SVL (RTaSV); length of rostral appendage (LRA); snout-casque length (SCL), measured from the tip of the snout to the posterior end of the casque; ratio of SCL to SVL (RSCSV); head width (HW); ratio of HW to SVL (RHWSV); distance from the anterior margin of the orbit to the snout tip (DOS); ratio of DOS to SCL (ROSSC); occipital lobes (OL) presence (+) or absence (–); length of lateral crest, starting from the eye horizontally (LC); length of temporal crest that starts upwards from the LC (TC); parietal crest (PC) absence (–) or presence (+); casque height (CH); dorsal crest (DC) absence (–) or presence (+); axillary pits (AP) of the forelimbs presence (+) or absence (–); diameter of largest scale on lower arm (DSA, defined as the area from the elbow to the manus in lateral view); number of scales on lower arm in a line from elbow to manus (NSA); scalation on lower arm (SL), heterogeneous (het) or homogenous (hom); number of supralabial scales (NSL; counted from the first scale next to the rostral to the last scale that borders directly and entirely (with one complete side) to the mouth slit of the upper jaw) on the right side; number of infralabial scales (NIL, analogous to the definition of NSL above, on the right side).

For skeletal morphology, X-ray micro-computed tomography scans (micro-CT scans) of the head of the holotype of *Calumma vatosoa* (MRSN R1628, locality Forêt de Tsararano) and of one presumed female *C. vatosoa* (SMF 26357, from Col Pierre Radama) were prepared. During micro-CT scanning, each specimen was placed in a sealed plastic vessel slightly larger than the specimen itself, with the head oriented upwards, and was stabilised with ethanol-soaked paper. To provide an undisturbed external surface of the head, it was ensured that the paper did not cover this area. Micro-CT scanning was performed with a phoenix nanotom m (GE Measurement & Control, phoenix|x-ray, Wunstorf, Germany) at a voltage of 130 kV and a current of 80 µA for 29 minutes (1800 projections). 3D data sets were processed with VG Studio Max

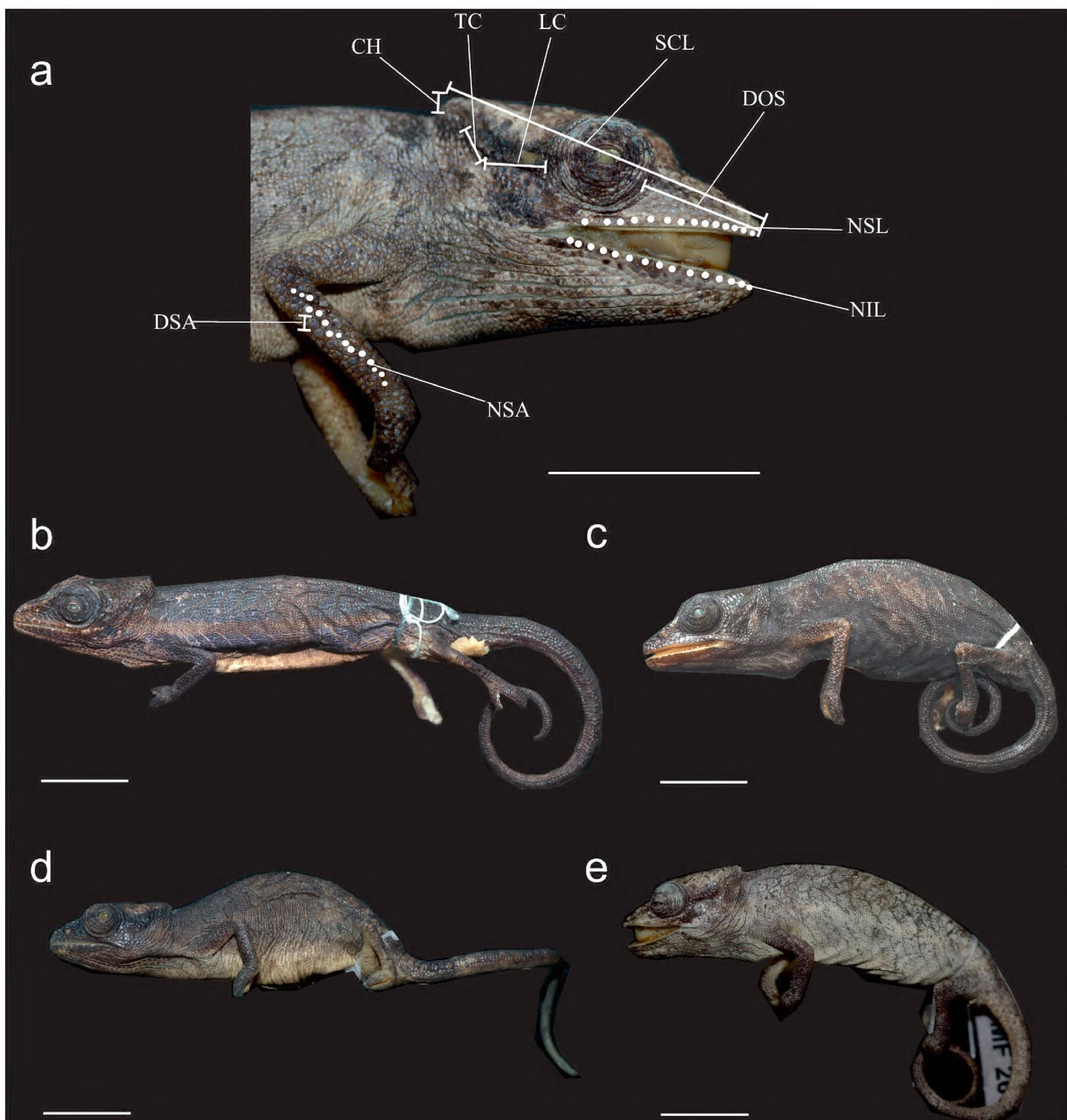


Figure 1. Preserved specimens of *Calumma vatosoa*; (a) Landmarks for morphometric measurements and pholidosis, shown in lateral view of the head region and forelegs of a female (SMF 26357, locality Ambatond’Radama); (b) male holotype of *C. vatosoa* (MRSN R1628, Forêt de Tsararano) in lateral view; (c) female (SMF 26359, Ambatond’Radama) in lateral view; (d) female (SMF 26358, Ambatond’Radama) in lateral view; (e) female (SMF 26357, Ambatond’Radama) in lateral view. Scale bar = 10 mm. See Materials and Methods for abbreviations.

2.2 software (Visual Graphics GmbH, Heidelberg, Germany); the data were visualised using the Phong volume renderer to show the surface of the skull. Measurements were taken with VG Studio Max 2.2. Osteological terminology follows Rieppel and Crumly (1997). Principal component analyses (PCA) was performed for 11 measurements/ counts (SVL, TaL, LRA, RSCSV, RHWSV, ROSSC, CH, DSA, NSA, NSL and NIL, see above) of all investigated specimens using the statistical analysis software PAST 3.08 (Hammer et al. 2001).

Results

External morphology of females. The three female specimens of *Calumma vatosoa* (SMF 26357, SMF 26358, and SMF 26359) are in a good state of preservation except a slit on the ventral side of the body (Fig. 1); SMF 26357 with mouth open and tip of the tongue between the jaws; SMF 26358 of smaller size and with poorly developed crests – presumably not full-grown; SMF 26359 blackened, presumably due to formalin injection.

Table 1. Morphological measurements of the male holotype and three female *Calumma vatosoa* and *C. peyrierasi* (one male, three females) in comparison with the species of the *C. furcifer* and *C. nasutum* group (represented as one male and one female if possible).

Species	Collection no.	Locality	Sex	SVL	TaL	TL	RTaSV	LRA	SCL	RSCSV	HW	RHWSV	DOS	ROSSC	OL	LC	TC	PC	CH	DC	AP	DSA	NSA	SL	NSL	NIL
C. furcifer group																										
C. andringitraense	ZSM 554/2001	Andringitra	m	45.7	48.4	94.1	1.06	-	16.5	0.36	3.5	0.077	5.5	0.33	-	-	-	-	0.2	-	+	0.3	27	hom	17	20
C. furcifer	ZSM 656/2014	Mahasoa forest	m	58.3	58.6	116.9	1.01	-	21.0	0.36	4.0	0.069	8.3	0.40	-	3.8	-	-	0.0	+	+	0.4	29	hom	21	20
C. furcifer	ZSM 657/2014	Mahasoa forest	f	61.2	54.3	115.5	0.89	-	19.7	0.32	5.1	0.083	8.2	0.42	-	3.6	-	-	0.0	-	+	0.4	25	hom	20	20
C. gastrotaenia	ZSM 1719/2010	Analabe forest	m	65.5	66.0	131.5	1.01	-	23.8	0.36	4.8	0.073	8.5	0.36	-	2.7	-	-	2.2	+	+	0.6	23	hom	17	18
C. gastrotaenia	ZSM 1718/2010	Analabe forest	f	61.7	53.9	115.6	0.87	-	19.7	0.32	5.7	0.092	7.9	0.40	-	-	-	-	0.0	-	+	0.4	22	hom	18	18
C. glawi	ZSM 2042/2008	Ranomafana	m	59.6	64.0	123.6	1.07	-	21.0	0.35	5.3	0.089	8.1	0.39	+	-	-	-	2.4	-	+	0.6	21	hom	16	17
C. guillaumeti	ZSM 1701/2012	Sorata	m	52.8	56.2	109.0	1.06	-	18.7	0.35	3.9	0.074	7.2	0.39	-	-	-	-	0.7	+	+	0.6	24	hom	15	18
C. guillaumeti	ZSM 1702/2012	Sorata	f	57.2	52.9	110.1	0.92	-	18.9	0.33	4.3	0.075	7.5	0.40	-	1.8	-	-	0.0	-	+	0.6	23	hom	15	16
C. cf. marojezense	ZSM 461/2010	Ambodivohangy	m	66.9	65.0	131.9	0.97	-	19.4	0.29	4.6	0.069	7.4	0.38	-	4	-	-	0.0	-	+	0.4	40	hom	17	18
C. tarzan	ZSM 219/2010	Tarzanville	m	72.6	78.0	150.6	1.07	-	22.6	0.31	4.1	0.056	9.3	0.41	-	3.2	-	-	0.6	-	+	0.5	33	hom	18	18
C. tarzan	ZSM 222/2010	Tarzanville	f	67.4	60.0	127.4	0.89	-	20.7	0.31	4.3	0.064	8.6	0.42	-	3.1	-	-	0.6	-	+	0.4	40	hom	20	20
C. vencesi	ZSM 50/2011	F. d'Amboloko-patrika	m	69.3	72.0	141.3	1.04	-	21.9	0.32	4.6	0.066	8.6	0.39	-	5.1	1.5	-	0.6	+	+	0.5	32	hom	18	20
C. nasutum group																										
C. boettgeri	ZSM 444/2000	Nosy Be	m	51.9	55.0	106.9	1.06	2.93	17.0	0.33	3.2	0.062	5.3	0.31	+	3.9	-	-	1.4	+	-	0.4	26	het	12	12
C. boettgeri	ZSM 441/2000	Nosy Be	f	45.5	43.4	88.9	0.95	2.73	15.3	0.34	2.9	0.064	5.0	0.33	+	3.2	-	-	1.4	-	-	0.4	27	het	12	12
C. fallax	ZSM 286/2010	Tsinjoarivo	m	48.8	57.3	106.1	1.17	3.60	16.6	0.34	3.5	0.072	5.2	0.31	-	2.7	2.0	+	1.9	+	-	0.9	11	het	14	15
C. guibei	ZSM 2855/2010	Tsaratanana	m	48.9	61.5	110.4	1.26	3.6	15.6	0.32	3.6	0.074	5.5	0.35	+	2.8	1.1	-	1.0	-	-	0.7	15	het	11	12
C. guibei	ZSM 2856/2010	Tsaratanana	f	45.9	46.5	92.4	1.01	1.3	14.9	0.32	3.1	0.068	4.8	0.32	+	2.6	1.0	-	1.0	-	-	0.6	17	het	12	13
C. gallus	ZSM 321/2000	Vohidrazana	m	45.0	43.7	88.7	0.97	9.7	15.4	0.34	3.1	0.069	4.8	0.31	-	2.9	-	-	1.1	-	+	0.7	16	het	15	14
C. linotum	ZSM 2073/2007	M. d'Ambre	m	59.6	64.8	124.4	0.92	4.50	16.8	0.28	3.1	0.052	5.2	0.31	+	2.3	-	+	1.3	+	-	0.8	16	het	-	12
C. linotum	ZSM 551/2001	Andampy	f	50.6	50.7	101.3	1.00	2.00	15.8	0.31	3.1	0.061	5.0	0.32	+	2.5	-	+	0.8	+	-	0.8	22	het	13	13
C. cf. nasutum	ZSM 924/2003	Andasibe	m	43.7	45.3	89.0	1.04	2.2	13.8	0.32	2.7	0.062	4.6	0.33	-	2.0	0.8	+	1.7	+	-	0.5	14	het	12	13
C.cf. nasutum	SMF 68273	Andasibe	f	46.2	45.8	92.0	0.99	1.8	12.5	0.27	2.8	0.061	4.2	0.34	-	1.5	-	+	1.5	-	-	0.6	15	het	12	12
C. vohibola	ZSM 645/2009	Vohibola	m	46.9	42.1	89.0	0.90	1.1	14.1	0.30	3.1	0.066	4.8	0.34	-	2.6	1.1	-	1.3	+	-	0.9	17	het	15	18
C. vohibola	ZSM 643/2009	Vohibola	f	45.5	40.4	85.9	0.89	0.3	14.2	0.31	2.3	0.051	4.7	0.33	-	2.7	0.7	-	1.3	-	-	0.8	16	het	14	14
C. vatosoa	MRSN R1628	F. de Tsararano	m	57.9	66.6	124.5	1.15	-	18.5	0.32	4.8	0.083	6.4	0.35	-	2.1	3.1	-	1.8	-	+	0.8	15	het	13	14
C. vatosoa	SMF 26357	Col Pierre R.	f	53.8	56.0	109.8	1.04	-	17.3	0.32	4.3	0.080	5.9	0.34	-	3.0	2.4	-	1.0	-	+	0.8	15	het	14	14
C. vatosoa	SMF 26358	Col Pierre R.	f	45.7	51.2	96.9	1.12	-	16.3	0.36	4.7	0.103	5.7	0.35	-	1.5	3.1	-	1.0	-	+	0.9	14	het	14	13
C. vatosoa	SMF 26359	Col Pierre R.	f	47.9	51.4	99.3	1.07	-	16.5	0.34	3.9	0.081	5.4	0.33	-	2.8	2.2	-	0.5	-	+	0.9	20	het	13	13
C. peyrierasi	ZSM 522/2014	Tsaratanana	m	51.1	55.2	106.3	1.08	-	19.9	0.39	4.9	0.096	6.5	0.33	-	3.6	2.4	-	2.5	+	+	0.7	18	hom	12	12
C. peyrierasi	ZSM 1726/2010	Tsaratanana	f	53.2	52.8	106.0	0.99	-	16.2	0.30	4.9	0.093	5.3	0.33	-	3.8	2.1	-	1.4	+	+	0.8	21	hom	12	12
C. peyrierasi	ZSM 1727/2010	Tsaratanana	f	56.0	54.6	110.6	0.98	-	15.6	0.28	4.9	0.088	5.8	0.37	-	3.5	2.2	-	0.9	+	+	0.7	17	hom	12	14
C. peyrierasi	ZSM 523/2014	Tsaratanana	f	56.4	52.5	108.9	0.93	-	15.2	0.27	4.8	0.085	5.4	0.36	-	3.2	2.1	-	1.2	+	+	0.7	22	hom	13	13

The morphological features of the three female *C. vatosoa* specimens ranged from: SVL 45.7–53.8 mm; tail length 51.2–56.0 mm; tail length 104–112 % of SVL; snout-casque length 16.3–17.3 mm, head width 3.9–4.7 mm; diameter of the orbit 4.7–5.1 mm; number of supralabial and infralabial scales 13 or 14; line of upper labials serrated; distinct rostral ridges that fuse on the anterior snout; no rostral appendage; lateral crest poorly developed and pointing straight posteriorly, fusing to form the poorly developed temporal crest that curves upwards and fading to the highest point of the casque; height of the casque 0.5–1.0 mm; no occipital lobes; no traces of parietal, dorsal, gular, and ventral crest; body laterally compressed with fine homogeneous scalation with the exception of the extremities and head region; legs with enlarged rounded tubercle scales (diameter 0.7–1.0 mm) bordering each other; heterogeneous scalation on the head; upper arm diameter 2.3–2.6 mm; axillary pits evident. Full morphological measurements in comparison to the holotype are provided in Table 1.

Skull osteology of the male holotype (MRSN R1628) (Fig. 2). Strongly developed maxillae extending anteriorly with tubercles at the lateral margin; small nasal bones (length 1.7 mm, width 0.3 mm) paired and meeting anteriorly; anterior tip of the frontal bone not exceeding more than a half of the naris and meeting the maxillae mid-dorsally; naris extending posteriorly up to the frontal bone (apomorphic state of *C. nasutum* according to Rieppel and Crumly 1997) and laterally bordered by the massive prefrontals with distal tubercles; prefrontal not meeting the maxilla; smooth frontal in the shape of a triangle, with a length of 8.4 mm and a width of 5.1 mm at the widest distance; parietal irregularly spotted with a few tubercles and tapering posteriorly from 4.2 mm (largest diameter) to 0.2 mm (smallest diameter); parietal meeting the squamosal and building the casque.

Skull osteology of the female (SMF 26357) (Fig. 2). Smooth maxillae without tubercles; narrow nasal bones (length 1.8 mm, width 0.2 mm) paired and meeting anteriorly; anterior tip of the frontal bone not exceeding more than a half of the naris and meeting the maxillae mid-dorsally; naris extending posteriorly up to the frontal bone and laterally bordered by the massive prefrontals with distal tubercles; prefrontal not meeting the maxilla; smooth frontal in the shape of a triangle with a length of 6.7 mm and a width of 4.9 mm at the widest distance; parietal irregularly spotted with a few tubercles and tapering posteriorly from 4.6 mm (largest diameter) to 0.5 mm (smallest diameter); parietal meeting the squamosal and building the casque.

The skull differs between the sexes in following characters (Fig. 2): The skull of the male holotype is ornamented with more tubercles and appears more robust than the skull of the female. Especially the shape of the maxilla differs with distal tubercles in the male and a smooth surface in the female. Further, the nasals are slightly broader in the male (0.3 mm vs. 0.2 mm in the female) and the

parietal tapers more sharply in the male, to 0.2 mm (vs. 0.5 mm). In conclusion, there is only weak sexual dimorphism in this species.

Colouration in preservative (Fig. 1). The colour of the specimens is faded after storage in alcohol for more than 80 years. The body of the female SMF 26357 is now of beige and bluish grey colour. A black stripe from the snout tip to the casque, crossing the eye, is clearly recognisable (a similar stripe is present in the holotype and on the photograph of the second individual, suggesting that it is characteristic for *C. vatosoa*). The eyelid is covered with light blue and purple spots. A midlateral white stripe runs from the upper lip to the pelvis on either side of the body. The body colour is bluish grey, becoming paler at the throat and venter (lacking a distinct white stripe) and darker at the extremities and the tail. On the legs there are blue tubercle scales, especially on the forearm region. The body is covered with a network of fine black lines. SMF 26358 is homogeneous bluish grey coloured with beige on the belly, the throat, and the inner side of the extremities. The legs bear blue-coloured tubercle scales; no other pattern is visible. The female SMF 26359 is completely coloured black, presumably due to exposure to formalin. Only the inner side of the extremities are of beige in colour. None of the three females shows any traces a yellowish spot on the flanks (which is recognisable on photographs of the living male holotype and the male photographed near Ampokafo). Neither the male holotype nor the three females show any pattern of a beige midventral stripe that is bordered by a white line on each side.

Distribution (Fig. 3). *Calumma vatosoa* is known from a small area of approximately 425 km² (Jenkins et al. 2011) in north-eastern Madagascar. The type locality is Forêt de Tsararano (14°54.8'S, 49°42.6'E, 665 m a.s.l.) between the Anjanaharibe-Sud Massif and the Masoala Peninsula (Andreone et al. 2001). Lutzmann et al. (2010) presented a photograph of one male individual from next to Ampokafo (15°15.4'S, 50°2.5'E, 400 m a.s.l.) which is located 50–60 kilometers south east of the type locality between Maroantsetra and Antalaha. We here add Ambatond'Radama (=Col Pierre Radama, 35–40 km north-east of Maroantsetra, N.E. Madagascar according to Viette (1991); coordinates approximately: 15°17.4'S, 50° 0.2'E) as a third locality of this species. Presumably *C. vatosoa* occurs in the forest among the three known localities.

Systematic position of *Calumma vatosoa*. Morphological measurements and pholidosis of *Calumma vatosoa* revealed substantial differences compared to the species of the *C. furcifer* group (see Table 1 for measurements). *Calumma vatosoa* differs from the species of the *C. furcifer* group in the following characters: heterogeneous scalation on lower arm vs. homogeneous scalation; larger diameter of tubercles on lower arm (DSA, 0.8–0.9 mm vs. 0.3–0.6 mm); lower number of scales in a line on the lower arm (NSA, 14–20 vs. 21–40); lower number of supralabials (NSL, 13–14 vs. 15–21) and infralabials (NIL,

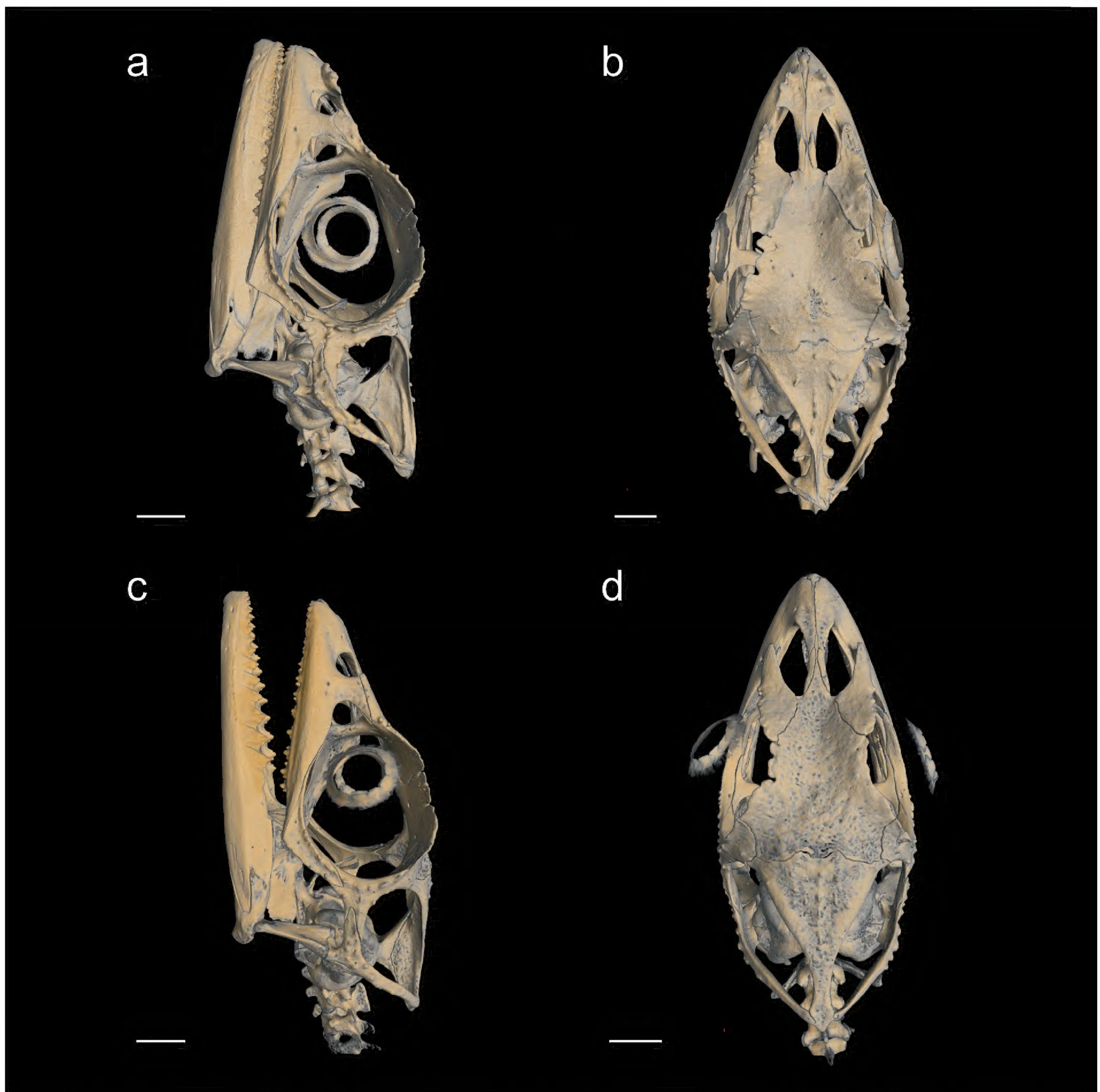


Figure 2. Micro-CT images of skulls of *Calumma vatosoa*; male holotype of *C. vatosoa* (MRSN R1628, Forêt de Tsararano) in (a) lateral and (b) dorsal view; female (SMF 26357, Ambatond’Radama) in lateral (c) and dorsal view (d). Scale bar = 2.0 mm.

13–14 vs. 16–20); longer tail relative to SVL, especially in the females (RTaSV, males 115 % vs. 101–107 %, females 104–112 % vs. 87–92 %); shorter distance from the anterior margin of the orbit to the snout tip related to snout-casque length (RSCSV, 0.33–0.35 vs. 0.33–0.42). In terms of colouration all species of the *C. furcifer* group show a distinct pattern of a beige midventral stripe that is bordered by a white line on each side. In *C. vatosoa* the venter is of paler colour than the body but it lacks any striped pattern.

These same measurements in the *Calumma nasutum* group were as follows: distance from the anterior margin of the orbit to the snout tip related to snout-casque length of 0.31–0.35 (RSCSV); heterogeneous scalation at the lower arm, consisting mostly of tubercles of large di-

ameter (DSA, 0.4–0.9 mm); number of scales in a line on the lower arm 11–26 (NSA); 11–15 supralabials (NSL); 12–15 infralabials (NIL; with an exception of the male *C. vohibola* with 18); tail length related to SVL with a maximum of 126 % (RTaSV) in a male *C. cf. guibei*. Occipital lobes (OL) and dorsal crests (DC) can occur in both groups (see Table 1). As it is typical for all other species of the *C. nasutum* group, *C. vatosoa* does not show any striped midventral pattern.

Despite the complete absence of a rostral appendage in *Calumma vatosoa*, our data demonstrate that this species is morphologically much more similar to the other species of the *C. nasutum* group than to the species of the *C. furcifer* group (see Table 1) and we, therefore, suggest transferring

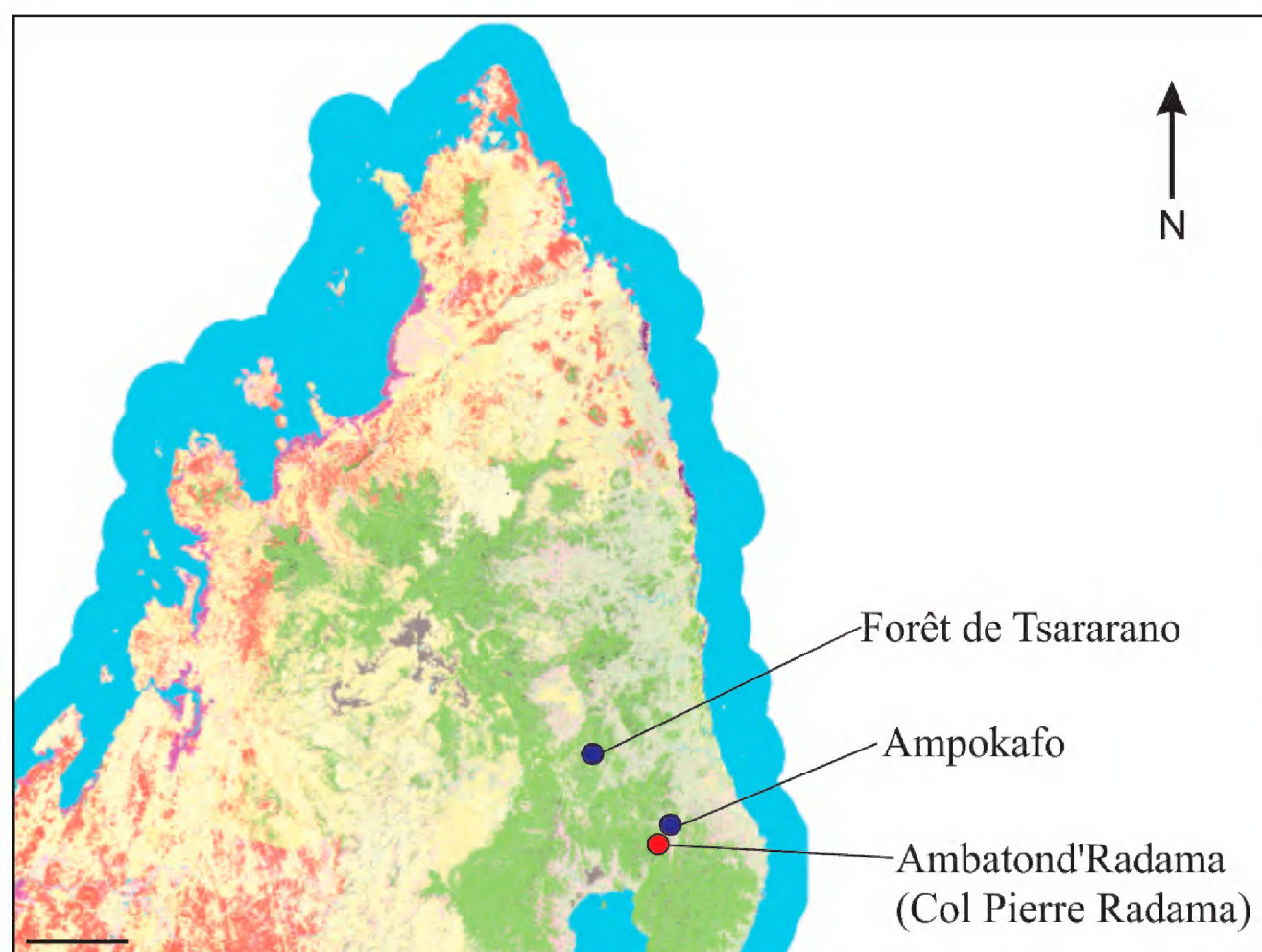


Figure 3. Map of northern Madagascar with previously known localities of *Calumma vatosoa* (purple circles) and the new locality of the females (red circle). Vegetation legend: humid forest (green), wooded grassland-bushland mosaic (beige), plateau grassland-wooded grassland mosaic (light beige), western dry forest (red), mangroves (pink), cultivation (light pink), littoral forest (purple), wetlands (grey). Scale bar = 50 km. Map from www.vegmad.org.

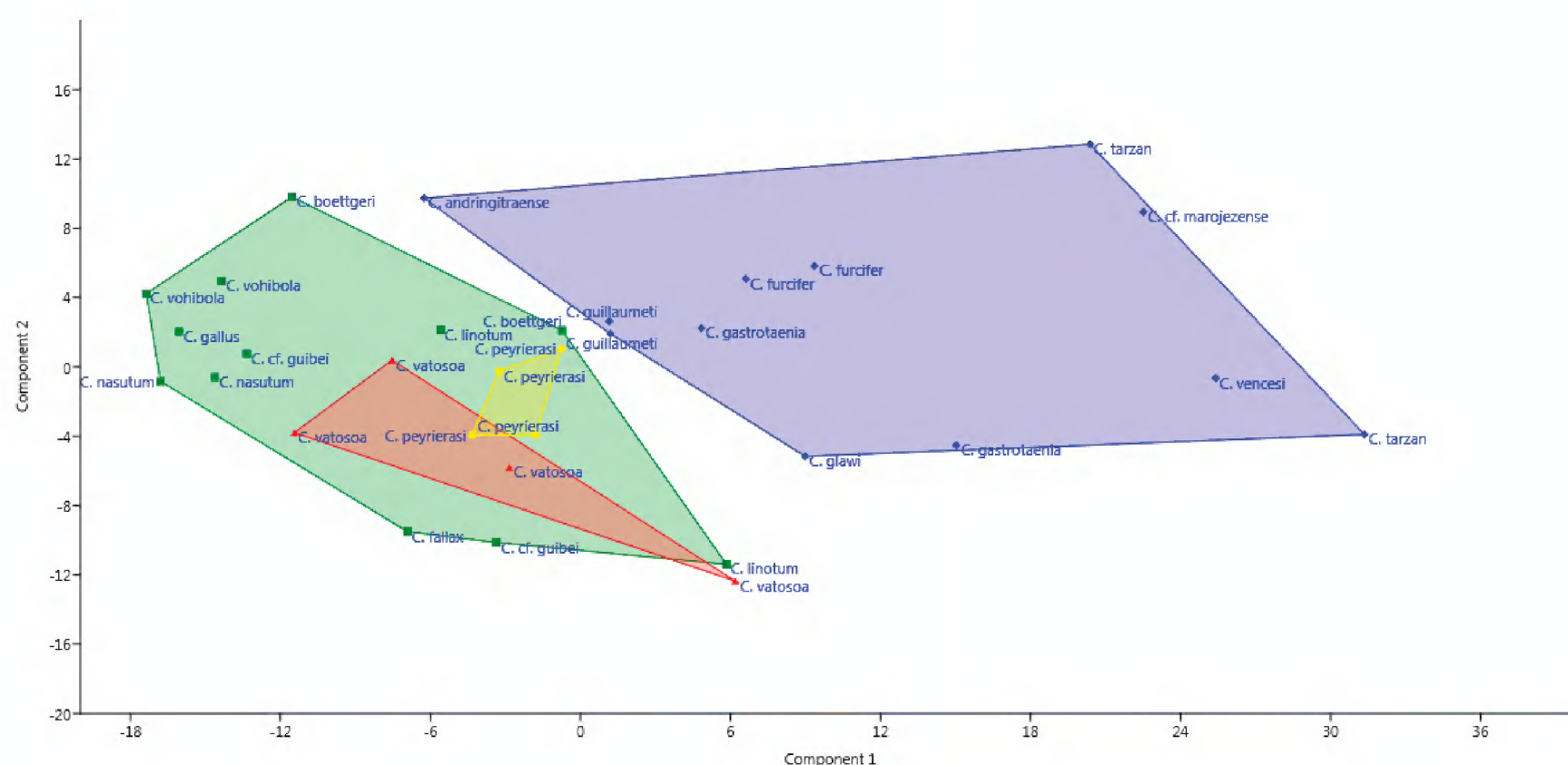


Figure 4. PCA of the species of the *Calumma furcifer* group ($n = 12$; blue diamonds), the *C. nasutum* group ($n = 12$; green squares), *C. vatosoa* ($n = 4$, red triangles) and *C. peyrierasi* ($n = 4$; yellow dots) based on 11 measurements/counts (SVL, TaL, LRA, RSCSV, RHWSV, ROSSC, CH, DSA, NSA, NSL and NIL of Table 1); Component 1 explains 73.93 % and Component 2 17.49 % of the variance.

it to the *C. nasutum* group. A PCA (Fig. 4, Table 2) clearly separates both groups explaining 73.93 % and 17.49 % of the total variance in PC I and PC II and places *C. vatosoa* within the *C. nasutum* group. Excluding body and tail length, important characters to differentiate between the *C. furcifer* and *C. nasutum* group (NSA, NIL, ROSSC and DSA) are shown in the graphs of Fig. 5, confirming that, *C. vatosoa* is placed among the species of the *C. nasutum* group.

Systematic position of *Calumma peyrierasi*. As an additional part of this work, the morphological similarity of *C. peyrierasi* to either the *C. nasutum* or *C. furcifer* group was investigated. The following morphological differences from the species of the *C. furcifer* group were identified (see Table 1): larger diameter of tubercles on lower arm (DSA, 0.7–0.8 mm vs. 0.3–0.6 mm); lower number of scales in a line on the lower arm (NSA, 17–22

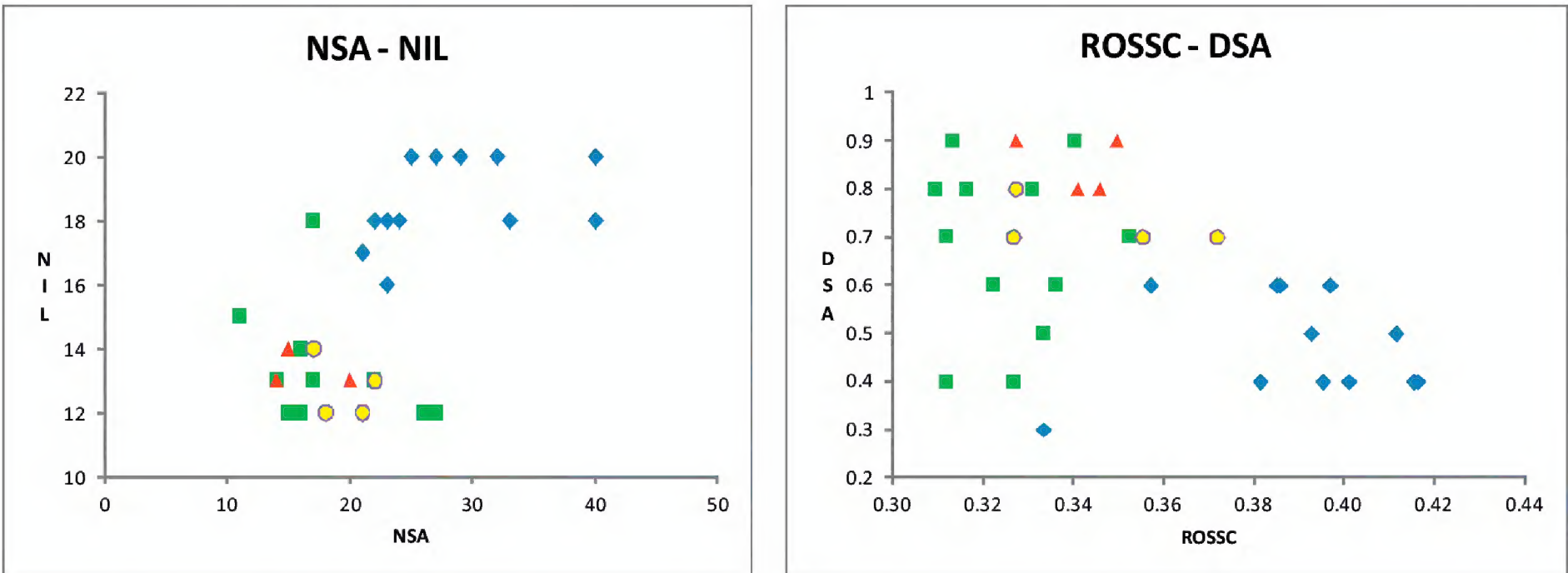


Figure 5. Important characters for the distinction of the *Calumma furcifer* group (n = 12; blue diamonds) and the *C. nasutum* group (n = 12; green squares), including the assignment of *C. vatosoa* (n = 4, red triangles) and *C. peyrierasi* (n = 4; yellow dots). Abbreviations: NSA, number of scales on lower arm in a line from elbow to manus; NIL, number of infralabial scales; DSA, diameter of largest scale on lower arm; ROSSC, ratio of distance from the anterior margin of the orbit to the snout tip and snout-casque length.

Table 2. Factor loadings for PC I–III for the investigated species of *Calumma furcifer* group and *C. nasutum* group (n = 28, Fig. 4)

	PC 1	PC 2	PC 3
SVL	0.6191	0.0197	0.4210
TaL	0.6271	0.5870	0.3080
LRA	0.0623	0.0506	0.1596
RSCSV	0.0001	0.0001	0.0001
RHWSV	0.0001	0.0004	0.0009
ROSSC	0.0019	0.0015	0.0045
CH	0.0155	0.0590	0.0350
DSA	0.0061	0.0171	0.0043
NSA	0.4238	0.7522	0.4997
NSL	0.1388	0.2008	0.4582
NIL	0.1429	0.2062	0.4914
Eigenvalue	161.885	38.306	9.210
%variance	73.928	17.493	4.206

vs. 21–40); lower number of supralabials (NSL, 12–13 vs. 15–21) and infralabials (NIL, 12–14 vs. 16–20). In terms of colouration, all species of the *C. furcifer* group show a distinct pattern of a beige midventral stripe that is bordered by a white line on each side. In *C. peyrierasi* there is only one distinct ventral stripe of white colour.

Compared to the species of the *Calumma nasutum* group the complete absence of a rostral appendage, the homogeneous scalation on the extremities, the predominantly greenish colouration, and the ventral stripe are atypical characters. Nevertheless, *C. peyrierasi* is placed among the species of the *C. nasutum* group in the PCA (Fig. 4) and in the graphs showing the distinctive characters of both groups (Fig. 5).

Discussion

In this work we have enlarged the knowledge of the poorly known chameleon species *Calumma vatosoa* and improved the systematics within the *C. nasutum* group and the *C. furcifer* group. On the basis of external morphology, osteology, and distribution we assign the specimens, which were collected by Bluntschli, to *C. vatosoa* instead of *C. linotum*, and provide the first description of females of this species. Andreone et al. (2001) tentatively assigned *C. vatosoa* to the *C. furcifer* group; however, after comparing the morphology and osteology of the investigated females and the holotype of *C. vatosoa* to all other species of the *C. furcifer* group, we demonstrate that the analysed characters of *C. vatosoa* are more typical of the *C. nasutum* group (Table 1) except for the absence of a rostral appendage and the presence of axillary pits. These characters appear to be variable, because axillary pits occur occasionally within the *C. nasutum* group (Prötzel, unpublished data) and the rostral appendage is strongly reduced in *C. vohibola* (see Table 1) and other members of the *C. nasutum* group (Prötzel, unpublished data). Molecular analyses are necessary to clarify the phylogenetic position of *C. vatosoa* in the *nasutum* group and if the appendage was secondarily reduced as was shown in *Furcifer campani* and *F. lateralis* by the phylogeny in Tolley et al. (2013). In the *C. nasutum* group the rostral appendage is relevant for sexual selection as demonstrated for *C. nasutum* (Parcher 1974), but sexual dimorphism in the length or the shape of the rostral appendage is weak or absent (e.g. in *C. boettgeri* according to Eckhardt et al. 2012). This is true for all members of the *C. nasutum* group with the exception of *C. gallus*. Accordingly the rostral appendage may play an important role in interspecific communication and species recognition as some species respectively candidate species of the *C. nasutum* group live sympatrically (Gehring et al. 2012).

The osteology of the skull of *Calumma vatosoa* is similar to other members of the *C. nasutum* group, e.g. the shape of the nasalia and the frontal (Prötzel, unpublished data) and shows only weak sexual dimorphism. In contrary to Mertens (1933) within the *C. nasutum* group the dorsal crest is not a constant character either, as this character can be present or absent in male *C. boettgeri* (Prötzel et al. 2015). Andreone et al. (2001) described the hemipenis ornamentation of *C. vatosoa* as exclusive within the genus *Calumma* due to their three pairs of rotulae. However, in our study on *C. linotum* (Prötzel et al. 2015) a hemipenis showed, in addition to the two pairs of rotulae that are typical for *C. boettgeri* and *C. linotum*, a third pair of rotulae. Consequently, even the morphology of hemipenes can be variable within a species, and three pairs of rotulae is not a unique character of *C. vatosoa*.

In conclusion, *C. vatosoa* is assigned as a member of the multifaceted *C. nasutum* group. A molecular study of the species would be helpful to confirm this assignment. Similarly, the morphological analyses of *C. peyrierasi* confirm its phylogenetic position in the *C. nasutum* group as revealed by Tolley et al. (2013)

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